

BIOLOGY AND TAXONOMY OF THE SOLITARY BEE,
PARASPHECODES FULVIVENTRIS (FRIESE).

By TARLTON RAYMENT, F.R.Z.S.

(Plates vii.-x., text-figs. 1-5.)

INTRODUCTION.

It has been evident to the author for many years that the generations of certain species are linked in some remarkable way with the cycles of the seasons. This concept was born after a study of the spectacular migrations of a number of animals, for it is certain that the presence of extraordinarily large numbers of animals connotes a superabundance of food and, since a number of herbivorous species are involved, plant-life must be the determining factor.

Since plants are the products of their ecology, it follows naturally that a superabundance of a species connotes favourable conditions for their development. Plant-life is so dependent on moisture that prolific growth is inevitably associated with ample rainfall.

The critical study of the biology of a species over a long period would assuredly also provide a key to the cycle of the seasons in a given locality. The species observed by the author are in several Orders, the emu (*Dromaius*); cockatoo (*Calyptorhynchus* sp.); capeweed (*Cryptostemma calendulaceum*); cypress-pine (*Callitris* sp.); gum-trees (*Eucalyptus* sp.); wattles (*Acacia* sp.); camel weed (*Teucrium* sp.); and many of the indigenous bees, all of which experience a period of superabundance followed by a recurrence of scarcity.

Certain wild-bees are exceedingly numerous in "good" years—that is, when an ample rainfall has produced a prolific growth of flowers. Since the eggs which developed the vastly increased numbers of bees were deposited 12 months previously, then some factor must have been operating at that period to bring about such a result. This is all the more remarkable when one remembers that not a single mother bee survives from one season to the next. The student finds it easy to postulate that the solitary mothers have some prescience of the nature of the ensuing season.

The indigenous bees are pre-eminently suitable for this research because they have been evolved together with the native flora and, therefore, are perfectly adapted to their ecology. Conversely, the introduced honey-bee, *Apis*, is almost valueless in this study, not only because of its unnatural concentration by man in large commercial apiaries, but also because of the fact that it is foreign to the flora, and, therefore, not adjusted to the ecology in which it now finds itself as the result of man's interference.

This maladjustment was observed in 1942, in New South Wales, when the author demonstrated conclusively that the many thousands of colonies of bees which were lost in the large commercial apiaries had died from a "deficiency" disease (malnutrition), brought about by one of the periodic failures of the white-box, *Eucalyptus albens*, to mature its male cells or pollen-granules, thus leaving the honey-bees without a supply of protein,

although there was an abundance of hydrocarbons (honey).—Rayment—in the press.

As part of the endeavour to find the "key" to the cycle of the seasons, the author investigated the biology of an exceedingly large "colony" of a solitary bee, *Parasphecodes fulviventris* (Friese), and as the life-history of any species in this genus was hitherto unknown, the author trusts that that will justify the publication of this paper. The taxonomic details have been forced upon the author by the circumstances.

The author is indebted to H. Womersley, F.R.E.S., of the Adelaide Museum, for his identification of the Collembolan specimens. The research was assisted by a small grant by the Trustees of the Commonwealth Science and Industry Endowment Fund, but the exigencies of war delayed the publication for several years.

TAXONOMIC POSITION.

Division ANDRENIFORMES.

Family ANDRENIDAE.

Subfamily HALICTINAE.

Genus PARASPHECODES Smith.

(Catalogue Hym., B.M. i., p. 39, 1853.)

Species *Halictus fulviventris* Friese.

Allgemeine Betrachtungen über die Bienenfauna Australiens, pp. 1-9, 1917.

Parasphecodes fulviventris Cockerell.

American Museum Novitates, No. 343, p. 16, March, 1929.

GROSS MORPHOLOGY.

Although Smith observed that these bees have a superficial resemblance to the European red-bodied *Sphecodes*, a parasitic genus, the author's investigations prove that *Parasphecodes* are industrious bees closely related to *Halictus*. The females have a rima or furrow on the apex of the abdomen, and most, if not all, of the males have a yellow mark on the clypeus; both characters being typical of *Halictus*. The glossa is short but acute in both sexes; there are four segments in the labial, and six in the maxillary palpi, as in *Halictus*.

The inclosed area of the metathorax exhibits even stronger rugae than *Halictus*, which sometimes has this sculpture quite weak, as in the *H. bicingulatus* group.

As Professor Cockerell, 1932, has observed, although the great majority of the species has a red abdomen, yet there is a series entirely black, and which are extremely difficult to separate generically from *Halictus*. However, Cockerell, 1930, proposed the subgenus *Aphalictus* for two species, *P. bribiensis* Ckll., and *P. bribiensiformis* Ckll., the females of which have bosses on the first two tergites.

The wing neurulation was studied in an exceedingly large series, and it exhibits the variations found in so many other bees. This generic character of Smith, therefore, may be disregarded. The genus was revised by Reinhold Meyer, 1920, but he had too few specimens to be adequate for the purpose. The author has a comprehensive collection, and he agrees with Cockerell, that *Parasphecodes* is extremely close to *Halictus*, but since he has found some divergence in the biology, it is better to retain the genus.

Almost confined to the eastern States of Australia, the genus is comprised of bees rarely more than 10 mm. in length. The males are smaller,

with longer antennae, and the labrum of the female has the triangular appendage characteristic of *Halictus*. The scopa of the female tibia is denser than that of *Halictus* and, generally, there is a larger number of hamuli on the posterior wing. The calcar of the female's hind tibia lacks the coarse teeth of *Halictus*, and the strigil of the anterior tibia exhibits no distinctive character, being almost identical in form with that of *Halictus*.

There are five species bearing a tubercle on the second sternite, and it is difficult to separate them by the descriptions, and, even when the specimens are before the student, the task is not easy, for the group demands critical study for accurate determination. The task was complicated by the presence of two species in the one great aggregation of "nests," *P. fulviventris* (Friese) and *P. arciferus* Ckll. The following synopsis will help students, and the specific descriptions of two allotypes are appended. All the males have, of course, a yellow clypeal mark. It is possible that *P. leptospermi* is the female of *P. hybodin*us.

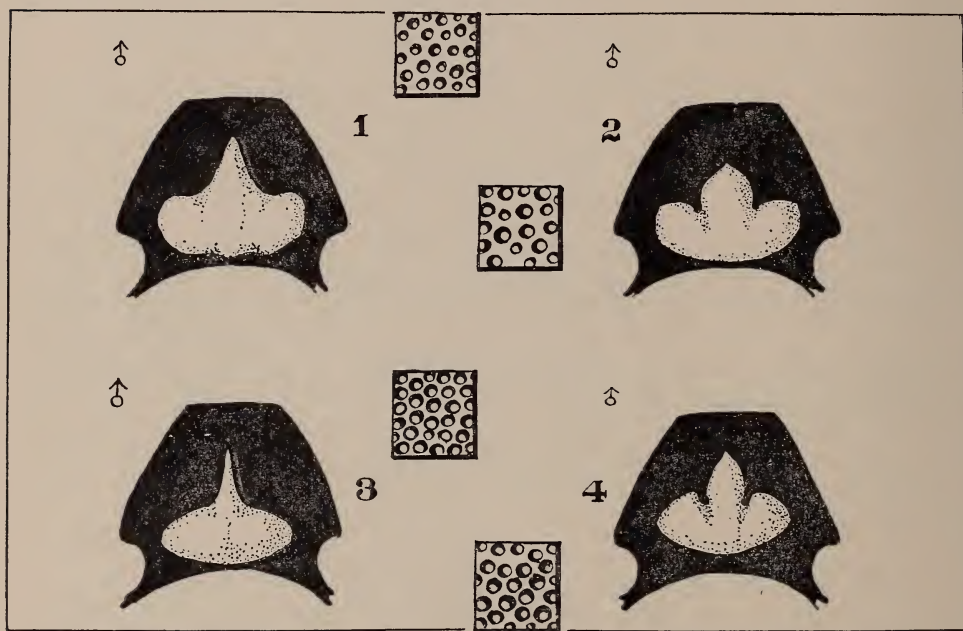


Fig. 1.—Clypeal marks and puncturation of the scutellum of males.

1. *P. fulviventris* (Fr.).
2. *P. anhybodin*us Ckll.
3. *P. arciferus* Ckll.
4. *P. hybodin*us Ckll.

There is a subspecies of *P. fulviventris*, with a bi-gibbose dull scutellum, and a minute tubercle; tergite one having no black basally; and tegulae polished black; hair of vertex and thoracic disc mixed black and white; second cubital cell higher than wide; nervures dark-amber, and pterostigma amber with a darker margin. This might be known as *P. fulvi-*

ventris proximus, subsp. nov. Collected by the author at Sandringham, Victoria, October, 1942.

Parasphecodes fulviventris (Fries).

Allotype, male: Length, 8 mm. approximately. Black and red.

Head long, with white hair on face; frons rugoso-punctate; clypeus shining, convex, an oval yellow mark with a small upward point; supra-clypeal area shining, coarsely punctured like the clypeus; vertex with blackish hair; compound eyes reniform, converging strongly below; genae rough, with a few long white hairs; labrum black; mandibulae black, reddish apically; antennae obscurely reddish beneath.

Prothorax not visible from above; tubercles heavily fringed with white hair; mesothorax bright, closely and coarsely punctured, but shining between, with blackish hair; scutellum similar; postscutellum rough, with white hair; metathorax with coarse radiating rugae, abdominal dorsal segments 1 and 2 with a fulvous band; 3 suffused with reddish; 1 and 2 closely punctured; ventral segments coarsely punctured, more or less banded fulvous and black.

Legs brown, with white hair; tarsi similar; claws reddish; hind calcar amber; tegulae brown, closely punctured; wings slightly dusky-yellow; nervures sepia; second cubital cell almost square; pterostigma sepia; hamuli ten.

Locality: Sandringham, Victoria, September 18, 1932 (Rayment).

Allotype in the collection of the author.

Allies: Taken in copula. The male is the smallest of the group.

Parasphecodes anhybodin Ckll.

Allotype, female: Length, 10 mm. approximately. Black and red.

Head broad, with scanty white hair; frons rugoso-punctate, but shining; clypeus polished; scattered large punctures, a depressed median line; supra-clypeal area elevated, with close puncturing; vertex with some black hair; compound eyes reniform, converging below; genae with long white plumose hair; labrum and mandibulae black; antennae black.

Prothorax with short moss-like white hair; tubercles polished, heavily fringed with white hair; mesothorax rugoso-punctate; coarse; with blackish hair on disc; pleura coarsely rugose; scutellum coarsely punctured, with black hair, like the mesothorax, bi-gibbous; postscutellum with black and white hair; metathorax with coarse radiating wrinkled rugae; abdominal dorsal segments 1-2-3 very deep-red; 1 more closely punctured; 3 deeply suffused; others shining black; ventral segments with reddish-suffusion on 1-2-3; with large blackish tubercle on sternite.

Legs blackish-brown, with white hair showing a dusky line; tarsi brownish, white hair; claws reddish; hind calcar pale-amber; tegulae black, polished, coarsely punctured; wings dusky apically; nervures brownish; second cubital cell very long; pterostigma brownish; hamuli thirteen, strongly developed.

Locality: Sandringham, Victoria, October 10, 1941 (Rayment).

Allotype in the collection of the author.

Taken in copula.

SYNOPSIS OF CHARACTERS OF THE FEMALES.

P. fulviventris (Friese).

Length, 10-11 mm. approximately. Clypeus with a median sulcus; scutellum with punctures smaller than those of the mesothorax; area of metathorax with strong rugae; little if any black on basal tergite; legs with white scopa; wings dark; pterostigma dark-brown; second intercubitus meets first recurrent nervure; large tubercle on sternite.

Melbourne; Sandringham, Victoria (Rayment).

P. arciferus Ckll.

Length, 9 mm. approximately. Clypeus with a median depression; scutellum with scattered large and small punctures, shining; area of metathorax with strong oblique rugae; a black patch on basal tergite; legs with brown scopa; wings paler; stigma dark-amber; second intercubitus just beyond the first recurrent nervure. Small tubercle on sternite.

Mordialloc; Sandringham, Victoria (Rayment).

P. anhybodinus Ckll.

Length, 10 mm. approximately. Clypeus with a depressed median line; scutellum with large punctures closely spaced, shining; area of metathorax with well-marked oblique rugae; black area on basal tergite; legs with smoky scopa; wings dark apically; stigma amber with dark margin; intercubitus just beyond the first recurrent nervure; second cubital cell large; small tubercle on sternite.

Cheltenham; Sandringham, Victoria (Rayment).

P. hybodinus Ckll.

Length, 10 mm. approximately. Clypeus depressed; scutellum with coarse punctures, shining; area of metathorax with large oblique rugae; black area on basal tergite; legs with whitish hair; wings dark apically; pterostigma dark-amber; second intercubitus meeting first recurrent. Large tubercle on sternite.

Windsor, Cranbourne, Sandringham, Victoria (Rayment).

P. leptospermi Ckll.

Length, 10 mm. approximately. Clypeus with scattered punctures, shining; scutellum bi-gibbous, shining, sparse punctures; area of metathorax with weak irregular rugae; tergites 1 and 2 red; legs with smoky hair; wings dusky apically; pterostigma dark-sepia; second cubital cell large; first recurrent almost meeting second intercubitus; tubercle on sternite large.

Brisbane, Queensland (Rayment).

LOCALITY.

An immense colony of *P. fulviventris* was discovered in the eastern bank, some 25 ft. in height, along the railway from Hampton to Sandringham, 10 $\frac{3}{4}$ miles from Melbourne. Since the line runs approximately north and south at this particular section, the eastern bank receives the full brunt of the afternoon sun, and is, therefore, a sheltered and warm situation, whilst its height ensures adequate drainage.

SITE OF THE NEST.

It is the second largest colony of bees reported in the literature of the APOIDEA, and is exceeded in area only by one, reported by Rica Erickson, 1941, of Bolgart, Western Australia. This observer described a wheat-field, a great many acres in extent, and which was perforated closely with the shafts and the shallow galleries of a small black bee. The author received specimens from this correspondent, and determined them as *Paracolletes pusillus* Ckll.

The area occupied by *Parasphecodes fulviventris* measured 600 ft. approximately in length. Owing to the steep angle of the bank, and the frequent passage of fast electric trains, it is impracticable to study critically the entire "face," which contains an enormous number of shafts. Since the geological strata vary with the height, there are fewer shafts on the "face" than on a narrow line, some 10 or so feet in width, along the flattish top, where the sandy loam is consistent throughout its entire length.

It was found, by actual count, that along the top the shafts averaged 30 to the square yard. Of this number 12 had tumuli of new damp sand during the month of February. The remaining 18 usually had the friable sand beaten down level, either by the wind, or the rain, so that the entrances to the shafts were just mere holes at ground level. In a "lean" year there was an average of only 12 shafts to the square yard.

GEOLOGY OF DISTRICT.

This is the well known "old red sand" formation (Tertiary) of the eastern shore of Port Phillip. At sea level is the reddish-brown rock, on which rests from 20 to 30 ft. of creamy-coloured decomposing sandstone known locally as "marl," and on top of all is the greyish sandy loam so characteristic of this area. In places, the yellow sand extends down for several feet, probably deposited as dunes, but generally it is from two to three feet in depth.

The bees appear to favour the even consistency of the sandy loam, where excavation presents no great difficulty. This choice, therefore, is in sharp contrast to that of *Euryglossa fasciatella* Ckll., which confines itself exclusively to excavating in the hard dry marl exposed along the sea-cliffs (Rayment, 1927, 1935).

Although the shafts of *P. fulviventris* are close, yet they are sufficiently distant from each other not to intersect, and there is no torturous plan wherein the galleries are mixed in inextricable confusion, as in *Halictus emeraldensis* (Rayment, 1937), which digs in tough red volcanic loam.

The nests are in ground similar in every respect to that favoured by *Paracolletes facialis* Ckll., and *P. tuberculatus* Ckll., and colonies of both these bees were found in flat situations a hundred yards or so distant from the bank (Rayment, 1931).

ECOLOGY.

The great difficulty experienced—the search extended over 20 years—in locating the shafts was due to the effective masking of the site by a dense growth of vegetation. Only when railway fettlers cleared the area, for a fire-break, was it possible to discern the shafts. The plants are characteristic of the Sandringham flora, the tallest being the tea-trees (*Leptospermum laevigatum* and *L. myrsinoides*); Nodding blue-bell

(*Dianella revoluta*); Heathy parrot-pea (*Dillwynia ericifolia*); Guinea flower (*Hibbertia stricta*); Club-rush (*Scirpus nodosus*); Pigface (*Mesembrianthemum* sp.); Small grass-tree (*Xanthorrhoea minor*); several small lilies; the introduced Flatweed (*Hypochaeris radicata*), and Capeweed (*Cryptostemma calendulaceum*) are growing closely together.

ARCHITECTURE.

The tumuli seldom exceed three inches in height, with a basal diameter of three inches, but they differ a trifle from those of *Halictus*, which have a central crater, like a miniature volcano. *P. fulviventris* constructs a cowl very similar to that of a *Cerceris* wasp (Rayment, 1947). The entrance is seldom if ever in the centre of the mound, but is placed more or less to one side, and, since the shaft invariably goes down at an angle, the moundlet becomes a kind of hood, as with *Cerceris*. The opening is usually to the north, but a few are a few points off to the east or to the west.

The material brought up from below is invariably fine greyish sand, slightly damp at first, but it soon dries, and is quickly dispersed in a few hours if windy. Most of the digging is done at night, and early morning; up to about 10 o'clock is the best time to observe the moundlets. The worker does not show herself whilst disposing of the spoil, for she just thrusts it up from below without opening or destroying the tumulus.

Very rarely there is a conical moundlet with two entrances only $1\frac{1}{2}$ inches apart, and the reason for this unusual structure is not clear, since the rule is one female to each shaft. In this they diverge widely from *Halictus emeraldensis*, and *Nomia*, where several females (sisters) use the same entrance (Rayment, 1943).

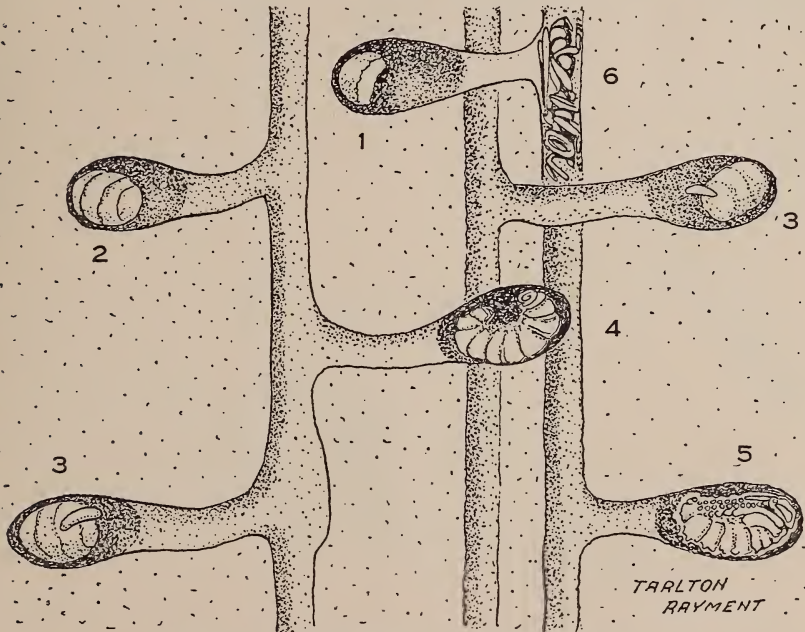
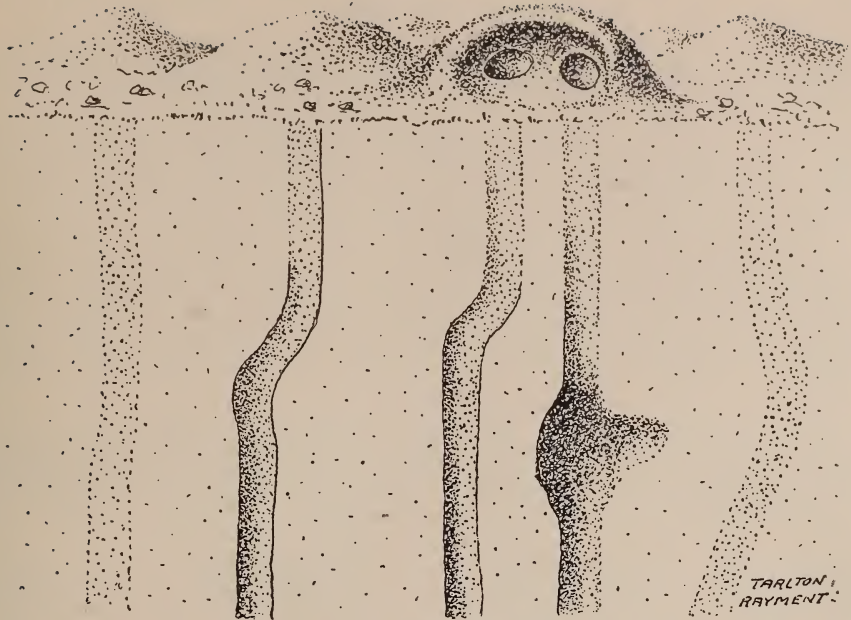
The shafts, with a diameter of 5-6 mm., go down at first at an angle of 45 deg., or thereabouts, for approximately five inches, the angled portion being 10 inches in the longest, and the shortest one only about $2\frac{1}{2}$ inches. The shafts then wind down more or less vertically for about 2 ft. From the main shafts are a number of short radiating galleries which end in single ovoid cells, and never in twin structures, as in *Cerceris*. The shafts take on a larger irregular diameter as they go deeper, as though they were extensions of original cells.

The great majority of the cells were discovered at about 2 ft. 6 in. from the surface. Generally, the upper 20 inches of sand are dry, and doubtless the bees go deeper to ensure the requisite humidity during the summer months, when the sand dries out rapidly. The shaft does not appear to receive any lining.

Short enlargements of the shaft occur here and there, but it would seem that these are more or less accidental, and concomitant on excavating in such friable material. The usual number of cells appears to be about eight, each of which measures 8 mm. at the long axis and 5 mm. at the short; a few larger ones measured 13 mm. and 7 mm. respectively.

The wall of the cell is covered with an extremely thin colloidal skin, which is licked on by the glossa, and when in the earth is of a dark umber-brown colour, but when exposed to the air it dries quickly, and becomes pale grey. Although the covering is so tenuous, yet it is thoroughly waterproof. The author has not yet found a solvent for this colloidal membrane.

When quite dry, the skin is exceedingly brittle, and tiny portions of it may be removed from the earthen wall, but it is impossible to secure a



Figs. 2. 2a.—Shafts of *P. fulviventris*.

2. Graphic diagram of tumuli on the surface; one showing two entrances under a cowl of sand.
- 2a. Graphic section of shafts and cells. (1) Partly formed cake of pollen. (2) Completed cake. (3) Cake with bee's egg. (4) Fully-grown larvae. (5) Pupa. (6) Adult female in shaft.

large piece. The lining is much more evident than the extremely thin skin of *Halictus*, where it is difficult to perceive any lining at all.

The author was not successful in finding a complete plug of mud or earth for closing the cell, as in *Halictus*, consequently, he would say that after the colloidal lining is drawn over to close to the cell, the short gallery is just filled in with loose sand, although the main shaft is left open. The entrance of which is, of course, easily closed by rain or wind.

In making very careful excavations, it was observed that cocoons of mutillid parasites appeared to be firmly surrounded by solid sand, for not the slightest trace of any connecting gallery could be found. Although the sandy loam is easy to excavate, yet its soft friable character makes extremely difficult the task of following down any one particular shaft with perfect success.

On October 15, 1941, Owen Dawson, R.A.A.F., of Clyde, Victoria, was building a house at Dandenong, some 22 miles east of Melbourne. On a clear hot day he observed a darting flight of insects about six inches above small shafts in the ground. They were probably females, although this observer did not catch any for determination.

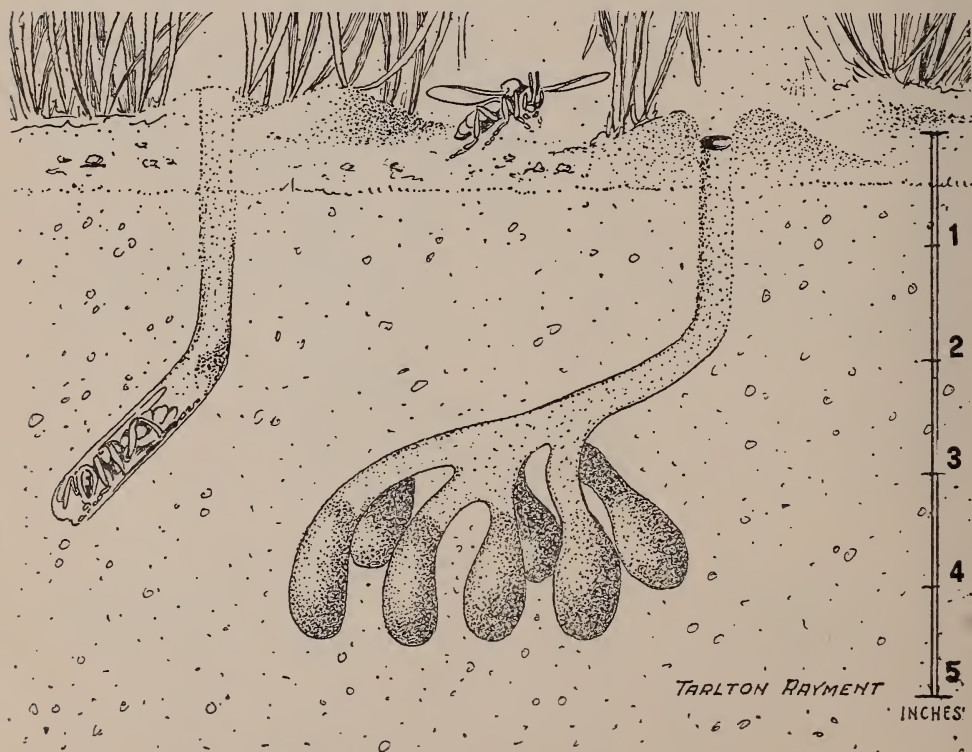


Fig. 3.—Graphic diagram of cluster of cells of *Parasphecodes subfultoni* Ckll. The arrangement approaches that of the bee, *Nomia australica*, and the wasp, *Cerceris*.

However, he made a closer examination of the site, which had a mere sprinkling of gravel over a rather loose black loam. There were no mounds of freshly excavated soil about the shafts, so the bees were probably beginning on the new chambers to receive the eggs.

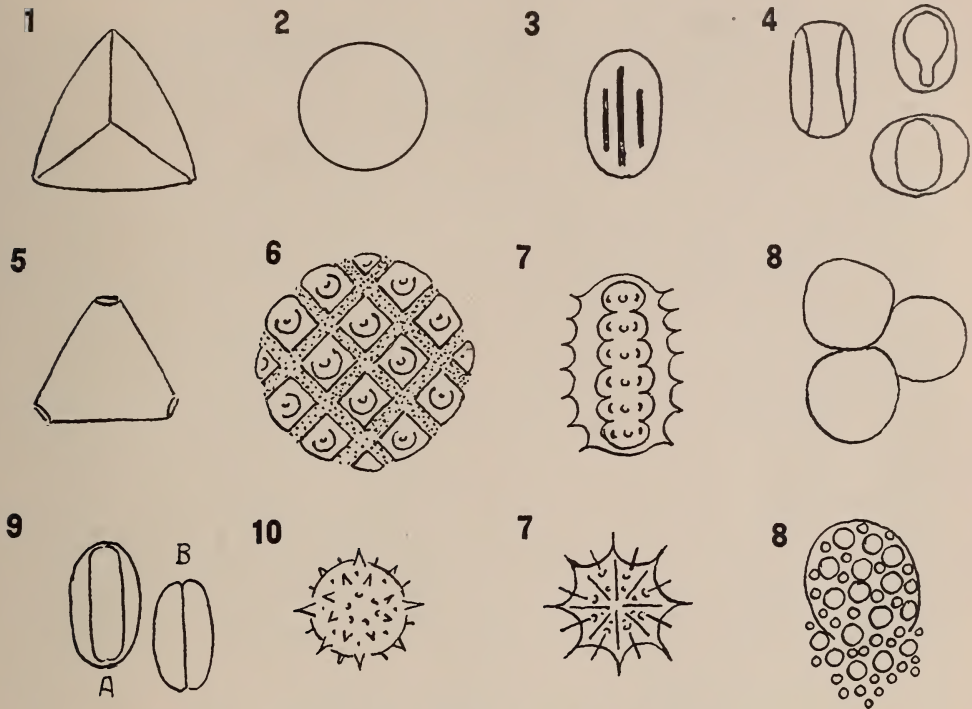


Fig. 4.—Granules from pollen-pudding of *P. fulviventris*.

1. Pollen-grain; probably from Tea-tree, *Leptospermum laevigatum*.
2. Large spherical grains not identified.
3. *Hibbertia sticta*.
4. Purple coral pea, *Hardenbergia monophylla*.
5. *Eucalyptus*; species uncertain.
6. Pollinium from Coast-wattle, *Acacia sophorae*.
7. Granule not identified and view of end.
8. Large fat-cells in fat-body of hibernating female, and a fat-cell breaking down; it is later absorbed.
9. (A) Not identified. (B) Parrot pea.
10. Spherical spiny grain, probably Flatweed; Compositae.

—Tarlton Rayment, del.

Dawson excavated a number of the shafts, and found the cells at a depth of only six inches, with short galleries opening off the main shaft in a more or less radial pattern. Each of the galleries terminated in an ovoid chamber, measuring 15 mm. at the long axis, and about 8 mm. at the short.

He described the new cell-lining as being of medium-grey colour, with

darker mottling; the old cells were just the colour of the earth, and he thought the cell wall would be less than 1 mm. in thickness. In a few of the new cells were traces of orange-yellow pollen, as though the bees had just commenced to store fresh provisions. Later, the author was able to verify these details.

A number of specimens was collected by this observer, and the author was able to determine them as *Parasphecodes subfultoni* Ckll., which was described from "Victoria" (F. E. Wilson, 1923). This species is considerably smaller than *P. fulviventris*, being about the size of *P. arciferus* Ckll.

Plants visited by *P. fulviventris* at Sandringham:—

Mexican Orange Flower	<i>Choisya ternata</i> (intro.).
Flatweed	<i>Hypochaeris radicata</i> (intro.), Compositae.
Capeweed	<i>Cryptostemma calendulaceum</i> (intro.), Compositae.
Marluck Tree	<i>Eucalyptus lehmanii</i> , Myrtaceae.
Yellow Gum or White Ironbark	<i>Eucalyptus leucoxylon</i> var. <i>macrocarpa</i> , Myrtaceae.
Swamp Mahogany	<i>Eucalyptus botryoides</i> , Myrtaceae.
Scarlet Gum	<i>Eucalyptus ficifolia</i> , Myrtaceae.
Red Gum	<i>Eucalyptus calophylla</i> , Myrtaceae.
Sugar Gum	<i>Eucalyptus cladocalyx</i> , Myrtaceae.
Purple Coral Pea	<i>Hardenbergia monophylla</i> , Leguminosae.
Guinea Flower	<i>Hibbertia stricta</i> , Dilleniaceae.
Parrot Pea	<i>Dillwynia ericifolia</i> , Leguminosae.
Cedar Wattle	<i>Acacia terminalis</i> , Leguminosae.
Coast Wattle	<i>Acacia sophorae</i> , Leguminosae.
Broom	<i>Genista</i> sp., Leguminosae.
Boobialla	<i>Myoporum insulare</i> , Myoporaceae.
Christmas Bush	<i>Bursaria spinosa</i> , Pittosporaceae.
Tea Tree	<i>Leptospermum laevigatum</i> , Myrtaceae.
Tea Tree	<i>L. myrsinoides</i> , Myrtaceae.

COMPOSITION OF FEBRUARY PUDDINGS.

No.	Eucalypts.	Acacia.	Flatweed.	Heath.	Undetermined
1	80%	10%		1%	9%
2	94%	1%	1%		4%
3	94%	1%	$\frac{1}{2}\%$		$4\frac{1}{2}\%$
4	70%				30%
5	96%	$\frac{1}{2}\%$			$3\frac{1}{2}\%$
6	90%	5%			5%

THE EGG.

Of all the bees' eggs studied by the author, only that of *Parasphecodes* has both ends inserted in the pollen-pudding; consequently, it is the most bowed of Australian bees' eggs, and resembles the handle of a minute basket. All of the new cells examined in this research contained eggs of this form, with the caudal end buried in the pudding.

The egg is crystal white, gleaming in the light, and measures approximately 3 mm. in length, with a diameter of 1 mm., when first laid—a large egg for such a small bee.

The chorion is extremely smooth, making it difficult to detect the exceedingly delicate hexagonal sculpturing, which is, of course, the imprint of the secreting cells lining the ovarian tubules, and only in critical side-

lighting under the microscope can it be detected with certainty. There is, however, a delicate striated pattern, and this is much more easily detected. It must be concluded that this striated sculpture is due to the condition of the larva within.

The egg increases in size before hatching; the caudal end is partially withdrawn from the batter, and the cephalic end rises a trifle from the pudding. Opaque white patches appear, and these, together with indications of segmentation, may be observed through the chorion. The head of the young larva does not reach to the end of the egg, leaving a space which remains pellucid as the body becomes more and more opaque. The caudal end of the egg is tipped with a hyaline agglutinative secreted by a gland at the apex of the female abdomen.

The exact time required for hatching could not be ascertained, but it appears to be about four days, when the egg splits open at the cephalic pole, and the chorion falls away, leaving the young larva occupying the original position of the egg. When first hatched, the larva exhibits a peculiarity in the spiracles, which are raised above the body, and with the tracheae resemble microscopic corrugated shafts or funnels.

The young larva lies quiescent on the pudding for a few hours, apparently sustained by the yolk of the egg, which it had ingested prior to hatching. The head is lifted up about 1 mm. from the surface of the pudding, and it rests in this position for several hours.

LARVAL FOOD.

The pollen-granules are carried on scopae of branched or forked hairs of several kinds; those on the coxae being five-branched; on the trochanters and femora they are long, slender, forked and curled; on the outer surface of the tibiae the hairs have one, two or three forks, but on the basitarsi they have five forks, and are shorter and stiffer. The bulk of the pollen, therefore, is carried on the legs, although there is a moderate amount transported on the scopa of the gaster, and, fortuitously, a few on the thoracic hairs.

The russet-coloured pollen-pudding is not truly spherical, dry and firm, like that of *Halictus*, but is much softer, since it contains more honey, and the base is widest, as though a soft sphere had gradually settled down on to a flat base. It is about 6-7 mm. in diameter.

Pollen gathered from the anthers is invariably lighter in colour than pollen taken from the body of the bee. It was observed that the harvester frequently moistens the anterior pair of legs with the glossa, and probably the pollen-rakes on the tarsi; this moistening no doubt assists dry pollen to cohere better.

Once again the author would stress the fact that, even in such primitive genera, the store is not a simple mixture of honey and pollen, but contains also a modicum of some biological secretion. This is probably secreted by the head glands, and added from the mouth during harvesting, and perhaps during the flight home, and later when the pudding is being formed. This substance, although small in quantity, is a vital factor in the development of the normal insect—a hormone not yet thoroughly investigated.

At present, research work on the food of bees is largely neglected, and until much more is done the phenomena of the various "castes," in the social bees, present a problem no less interesting than the genetical mechanism in such parthenogenetic genera as *Halictus* and *Nomia*.

The larva, when eating, does not sweep regularly across the pudding, taking off a slice as it goes, which is the manner of *Halictus emeraldensis*. The larval jaws are exceedingly sharp and needle-like, but the larval ingestion is like a toothless human "mouthing," a spoonful of porridge, and the baby eats whatever portion is within reach.

About 8-9 days are required for the complete ingestion of the pudding, when the larva shows a dark lead-coloured streak along the dorsal surface, and a similar dark patch marks the accumulation of the residues in the sac before the complete junction of the mesenteron and the proctodeum is effected.

About five days later, when the alimentary canal is complete, thirty or so dark-brown stercoral pellets are expelled in a more or less moniliform chain. Thereafter, the larvae are crystal white, of virgin purity. The pellets were examined under the microscope, and a number exhibited minute bosses of clear, smooth amber.

The excreta were carefully washed away, and several slender horn-like capsules were recovered. On breaking these on a micro-slide, a very large number of oil-globules escaped. It would appear that the larvae of *Parasphecodes* cannot use all the natural oils in the pollen-granules, and the great excess is voided in these curious capsules. The author has not observed these formations in the stercoral pellets of any other genus, although there is often a percentage of oily matter present. The author did not determine whether they were peculiar to one sex only or not.

Snodgrass, 1925, says "the fats are apparently but little used by the bees. Though pollen is rich in oil, much fatty material accumulates with other refuse in the intestine, as shown by Petersen." The blood of the hibernating adult bees contains many oily globules which appear to be liberated from the fat-cells, and Straus, 1911, says the larva of the honey-bee stores more glycogen than any other free-living animal.

The fat-cells of the "hibernating" females contain large oil-globules, and the cells themselves disintegrate, and so liberate the globules into the blood. Whether or not this apparently natural dissolution of the fat-cells is necessary for nourishing the body during the semi-hibernation is not known, but there is no doubt that the fat-cells disintegrate as a natural process as maintained by Snodgrass for the honey-bee.

The larva exhibits a number of nodes, and in the pupal stage these quickly develop into a series of long "studs" or tubercles, the most prominent being on the scutellum and postscutellum, but the hind margins of the tergites are also tuberculate, each having up to ten. These nodes are characteristic of Halictine pupae, and it must be concluded that *Parasphecodes* is exceedingly close to *Halictus*, although the nodes are not so prominent. The ventral node, a specific character, soon appears. Antennae, legs, and tergites 1, 2 and 3 are still drab when the head and thorax are quite black, as are tergites 4, 5 and 6.

The postscutellar nodes persist in the adults in the genus *Nodocolletes* Raym., 1931, as large concave bifid processes, but they disappear altogether in all other Australian bees studied by the author. The spines of the coxae are, with few exceptions, retained by adults in the leaf-cutters, Megachilinae; but disappear entirely in *Apis*, the hive-bee. The anterior tibial spine is retained by all bees, and ultimately becomes the strigil, or antenna cleaner. The spur of the median tibia develops into a calcar in all bees.

Larvae which ejected the stercoral debris on February 18 shed a larval pellicle on the 22nd, probably the third ecdysis, but, at that date, there were not any signs of colour in the body. A creamy opaque tint appeared on March 5, and the ocelli and the compound eyes turned the palest purple. Five days later, fine blackish margins appeared on the abdominal segments, the head exhibited a pale slaty colour, and then the thorax darkened. On March 18 another pellicle was shed, and the pupa changed slowly to dark lead-colour, except the red parts of the abdomen, which were still pale-cream in tint, the red parts coming last of all. The wings remained milky. The blackish suffusion strengthened quickly, and, two days later, March 20, the final pellicle was shed, and the insects were ready for flight. All these proved to be males, and the period of development was 56 days.

A generation of males and females, maturing in the field, about March 20-22, appeared on the trees at about the same date as the laboratory specimens emerged, so that development in the laboratory must have been normal, since it corresponded with what took place in the field.

BEHAVIOUR OF THE INDIVIDUAL.

The pupa twists and wriggles until the final skin is cast off, and it rests in the cell for a day or two, during which time the wings lose their milky tint and become suffused with blackish.

The insect then begins to tunnel out along the short gallery, which is filled with loose sand. Stubborn grains are wrenched out with the mandibles, and the more friable material is thrust behind with the legs. The exit presents no great difficulty owing to the complete absence of stones. The main shaft is ascended just as easily.

Emerging to the light at the surface, the bee rests in the sun for a minute or two before taking wing. Almost immediately a rather chalky-looking liquid is voided, and which, on testing with a litmus strip, gives a strong acid reaction. This is very marked in the genus *Hylaeoides* (Rayment, 1940), which voids a very large quantity.

The males take off for the blossoms to refresh themselves, and make little attempt at orientation, nor is there much need to do so, since the site of the colony is so extensive, and the soil varies not at all over the whole area; few ever return.

Among the flowers the sexes meet, and copulation frequently takes place amid the actual stamens of the gum-blossoms. Other species of *Parasphcodes* were observed copulating on the much smaller flowers of *Boobialla* (*Myoporum insulare*).

Refreshed with the nectar, the female returns to the colony site, and immediately seeks a satisfactory place to commence digging. After a few grains have been removed with the mandibles, the mother frequently abandons her first choice, and recommences a few inches away, although there are no differences apparent to the observer in the two places.

The excavating is effected with the mandibles and the legs, and the damp pellet—approximately a match-head in size—is hauled to the surface, and pushed out, without exposing the worker. The tumulus grows from beneath as the spoil is added to the base. During cold weather, the females remain in the cells, perhaps for three or four days.

The female rarely sits at the portal of the shaft, as is the habit of

many Halictine bees, and the only time she appears to do so is when something moves in the vicinity as she is about to depart. She will then close the aperture with her head, but any untoward movement will send her down the shaft instantly.

The males have not been observed in the vicinity of the shafts after their initial departure, but, at evening, the males of the colony assemble and form a rather compact, but unsymmetrical cluster on a twig of a shrub for mutual warmth.

These aggregations are no doubt an elemental stage of the clustering instinct of the honey-bee, *Apis*, and similar congregations of males have been observed by the author in several other genera, for the instinct is very strong in the Apidae.

In another Halictine genus, *Nomia*, the males of three species were observed to cluster together at evening. One such aggregation contained the large *N. ruficauda*, *N. gracillus* and the smaller *N. flavoviridis*; all these are more or less metallic in colour. Large "swarms" of *N. australica* have been observed, and Doctor Lieftinck, Buitenzorg, Java, N.E.I., sent a photograph to the author showing a cluster of *Nomiine* males. The clustering instinct is very strongly developed in *Paracolletes*, and large "swarms" of *P. plumosus* Sm., and *Heterocolletes capillatus* Raym., 1935, have been observed by the author.

The clustering of the males is a Halictine habit, and this formation may be continued throughout the day in adverse weather, but generally it is broken very early in the morning, when the bees depart for the flowers.

Owen Dawson reported to the author that when stationed at Rocklands, Victoria, with the R.A.A.F., he passed under a low branch of a gum-tree, and immediately a swarm of small red bees took wing. However, they soon reformed the cluster, after he had passed. He repeated this several times, and collected a dozen or more of the bees, all of which were males that agreed very well with the description of *P. sextus* Ckll.

The female experiences little difficulty in returning to her own shaft, although there are so many close at hand. The natural conditions are such that plants of some kind grow close to the aperture, and no doubt these serve as landmarks to guide the homing bee. Even the total clearing of the site did not create any great difficulty, and the bees alighted within two or three inches of the aperture, which they soon located, probably by scent, as they often come up against the wind.

The nectar, of course, is carried in the honey-sac, and is "licked" up from the nectary of the flowers by the pointed glossa. Just how this is effected is not quite clear, but the hairy tip of the "tongue" lies flat on the surface of the ovary of the flower and is moved backwards and forwards very rapidly, without being turned over. The large paraglossae and the maxillae appear to assist in the ingestion of the nectar, but it is extremely difficult to determine the actual functioning of the complicated mouth-parts.

The author has observed both *Parasphecodes* and *Halictus* ripening the newly-gathered nectar by sitting in the warm sun and extending the mouth-parts. The bee exudes a large drop of nectar and, since the submentum is "hinged" at the base, a rapid extension and contraction of the liquid takes place, and it may be seen to thicken during the process. Park,

1932, claims that manipulation by the mouth-parts plays an important part in the ripening of nectar by the honey-bee.

Although many Australian wild-bees are endemic, confining themselves to one botanical species, this is not true of *Parasphecodes*, for it visits a wide range of plants, as the botanical list indicates. Like the hive-and most wild-bees, the insect confines itself to one species whilst harvesting, for the author finds no admixture of pollen-granules on the body—except, of course, an accidental one, probably adhering from a previous journey. No matter whether the pollen be bright-orange (Flatweed), or cream-colour (Eucalypts), the puddings in the cells, during February, are invariably olive-green in colour. There is not any after-feeding, and the original pollen-pudding is the total amount of food provided for each larva.

ORDER OF THE GENERATIONS.

The research demonstrated that three generations are present in this species during the season: A spring one of males and females; the second, a summer brood of males and females; the third one, of males and females, appears late in autumn. The individuals of the three generations are necessarily early and late in emerging, as the case may be, and it is unwise to fix specific dates for their appearance.

The bees emerge to flight in spring from, say, September 15 to October 1, the second half of which is spent in working at digging and provisioning cells, and depositing eggs; the flying bees then disappear.

During November and December, the larvae are developing in the cells in the earth. In the early days of January, a new generation of males and females is a-wing, and the latter portion of January is spent in labour. During February and early March, another generation is developing in the earth. These males and females emerge, and are a-wing during the latter half of March, and there are many matings during the early part of April. The males then disappear—succumbing to the cold during early May. The larvae develop in the earthen cells to hibernate over the winter, and emerge during the ensuing spring. The phenomenon of parthenogenesis is not present in this species.

SEMI-HIBERNATION.

Numbers of "nests" were excavated by the author during June and July. The bees appeared to be perfectly developed in every way, and when uncovered to the light of day immediately began to dig into the loose soil about them. At first they are lethargic, but their movements soon quicken. At no time are they so active as summer females surprised in their cells.

It is quite clear that these wintered females are the progeny of the mothers of the previous April, and which were in the company of many males on the flowers of *Eucalyptus leucoxydon* var. *macrocarpa*, and *E. calophylla* var. *rosea*. Many copulations of the sexes on the blossoms were recorded on March 21, 1942, and the mated mothers were digging energetically down below, for moundlets of new yellow spoil were observed up to the 1st of April.

The breeding experiments demonstrated that up to 56 days are required for the development of the February-March females; consequently, eggs deposited early in April would produce the last brood for the season, and the latest would mature before July. They then pass through the winter in their cells in a state of semi-hibernation.

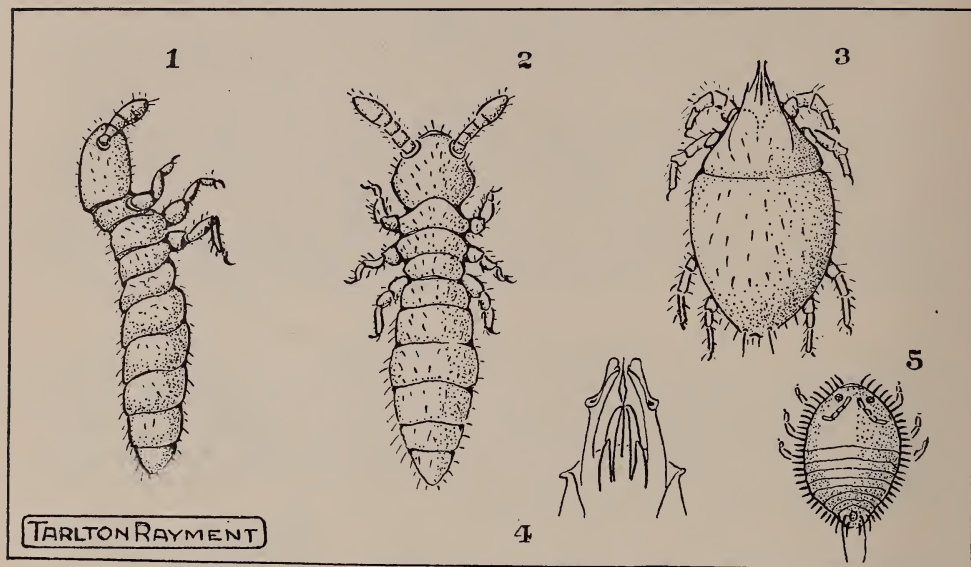


Fig. 5.—Inquilines and parasites of *P. fulviventris* (Fr.).

1. Lateral view of Collembolan, *Onychiurus fimetarius* L.
2. Dorsal view.
3. Acarid mite, *Caloglyphus berlesii* (Michael).
4. Stylets of the mite.
5. Remarkable insect taken from the gena of *Parasphecodes subfultoni* Ckll. This is probably a Coleopteran, but it was not studied.

Microscopical examination of the abdominal organs disclosed that the honey-sac had never contained any food, nor had the stomach (ventriculus), which was quite empty. A remarkable feature was found in the Malpighian tubules; these are lined with a bright-yellowish substance, discharged almost immediately after the insect first takes wing. Thereafter, the tubules are practically colourless. The ejected substance represents the body-waste accumulated during pupal development.

PARASITES AND INQUILINES.

It was observed in the laboratory that numbers of the bees' cells were visited by minute white insects, resembling Collembola, but minus the abdominal spring of that genus. These insects averaged about 1,000 microns in length and were submitted to H. Womersley, of the South Australian Museum, who determined them as *Onychiurus fimetarius* L., which has a world-wide distribution in the humus of soil.

The author has no doubt whatever that in the earthen chambers the moisture would soon bring about an insanitary condition only for the activities of these insects and certain Acarid mites. It was observed in the field that none of the cells contained any stercoral or other refuse; indeed, even the cast skins of the several ecdyses soon disappear.

There is a symbiotic relationship that is distinctly beneficial, if not

essential, to the welfare of the larval bees. There is not the horde of acarid mites present in *Halictus emeraldensis* (Raym., 1937), but the same work is accomplished by these insects and mites, for the cells are always immaculate and entirely free from moulds.

The parasites' visits to the cells are fairly regular, but, as the insects exhibit a strong aversion to light, it was possible to observe them only by surprise; a very unsatisfactory method at any time. However, the author did not succeed entirely in defeating the tropism; consequently, the observations are not as complete as he would like them to be.

No Acarid mite was observed in the numerous cells examined, but many were discovered in the field at Rocklands (December, 1942), on the larval bees of *P. sextus*, but one was taken from the earth nearby. This mite measured 750 microns in length, and was determined by Womersley as *Caloglyphus berlesei* (Michael), which is often found in termitaria and decaying organic materials.

A very remarkable minute ovoid insect, some 380 microns in length, was removed from the gena of one specimen of *P. subfultoni*, collected by Owen Dawson, at Dandenong, Victoria, but the author has no other information on the specimen, and for the time being defers a discussion on its taxonomic position.

A MUTILLID WASP.

During the excavation of the site of the nests, large numbers of small drab cocoons, some 3 mm. in length, were collected at various levels. These appeared to be encased in solid earth, since no signs of cells could be detected.

They were removed to the laboratory, and critical examination revealed them to be the thin skin-like cocoons of a small Mutillid wasp. The large numbers of these indicate that *Parasphcodes* is heavily attacked by Mutillids.

The behaviour of these parasites has been closely observed by the author, and the procedure does not vary, whether it be on *Halictus* or *Parasphcodes*, the Mutillid searches the surface of the site, and, discovering a shaft, does its utmost to scent the presence of the bee.

Should the rightful occupant be absent, the Mutillid runs down the shaft, and, quickly depositing her egg on the body of the larval bee, hastily returns to the surface. Should the shaft contain a bee, the parasite immediately beats a hasty retreat to try her luck elsewhere. Sometimes the usurper is chased out by the irate mother. The ovipositor of the Mutillidae is very short, but the parasite is close to its host's body.

A number of larger reddish cocoons were obtained, but these were all empty, making it impossible to determine which insect made them, but as they were numerous, it appears that another parasite is present at some period, and the author would suggest that it is an Ichneumonid wasp, perhaps a Cryptine, in the genus *Labia*, as an undetermined species was observed at no great distance from the site. The biology of the earth-digging bees in the subfamily Halictinae is an extremely difficult study; a fact often stressed by the late Professor W. M. Wheeler.

AN INTERNAL PARASITE.

(A Nematode Worm.)

Whilst dissecting some of the hibernating females in isotonic salt solu-

tion, nematode worms were observed swimming among the organs with an eel-like motion. The parasites were very small, measuring 650 microns in length, with a diameter at the thickest part of 25 microns. Although the host had been killed with ether, the parasites continued to be exceedingly active in the isotonic solution until killed instantly by a drop of acetic acid.

Although the locomotion is eel-like, the worms frequently whip themselves into a circle, or even a figure eight conformation, when they remain still; after a second or two, the quick undulating motion is resumed.

It was observed that nematodes were not enclosed in any part of the alimentary canal, but were swimming freely among the organs. Indeed, so far as could be ascertained, the canal had not been punctured, but it was noted that the whole interior of the abdomen was markedly deficient in blood. This peculiar dryness was detected in other hosts of the parasite.

Large numbers of larvae and also active summer female bees were dissected, but nematodes were not observed in any. It would seem, then, that the parasites somehow gain admittance to the abdomen during the long period of semi-hibernation over the winter months, but just how they enter the body of the bee was not determined.

The organs did not appear to have suffered any structural injury, but the loss of so much blood and fat must undoubtedly affect the vitality of the bee, and perhaps preclude its emergence in the spring. A percentage of such infected females may perish in their natal cells, but no dead bodies were discovered in any of the nests excavated by the author. Externally, there is nothing whatever about the body of the bee to indicate the presence of the parasites within the abdomen.

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EXPLANATIONS OF PLATES AND FIGURES.

Plate vii.

Anatomy of *P. fulviventris* (Fr.).

1. Adult female *P. fulviventris* (Fr.).

2. Rugose sculpture of metathorax.
3. Bidentate mandible.
4. Nodulose second sternite of female.
- 5, 6, 7. Fourth, fifth and sixth sternites.
8. Fifth tergite of female showing the apical rima of the Halictine family.
9. Sixth tergite showing plate under rima—all abdominal plates as pressed flat by the cover-glass.
10. Labrum of female has the angular appendage of the Halictine family.
11. Fifth tarsal segment with anguiculi and empodium.
12. Sculpture of clypeus showing the median depression.
13. Hairs on wing-surface.
14. Slender curled hairs of femora and trochanters.
15. a.b.c. simple, bi-forked, and tri-forked hairs from outer side of tibiae. d. five-forked hair on outer side of basitarsi. e. compound hairs of coxae.
16. Rugoso-punctate sculpture of frons.
17. Eleven hamuli of hindwing.
18. The small brush, distally on basitarsus, is another Halictine character.

Plate viii.

Larval development of *P. fulviventris* (Fr.).

1. Caudal end of the bowed egg is inserted in the soft pudding.
2. The hexagonal pattern on the egg is almost invisible; the striated pattern is more evident.
3. On larvae three days out of the egg—
4. The tracheae appear to be above the spiracles.
5. The larva after the pellets have been ejected.
6. Stercoral pellets showing tips of the oil capsules (a).
7. Nodes on scutellum and postscutellum of pupa before pigmentation.
8. Hind margins of tergites are tuberculate, as in *Halictus*.
9. Pupa before pigmentation.
10. The developing mouth-parts.
11. Invagination of apical segments of male abdomen during pigmentation.

Plate ix.

Anatomy of *P. fulviventris* (Fr.).

- 1, 2, 3. Motions of Nematode worm parasite.
4. Lateral view of open proventricular valve. Arrows indicate direction of flow of honey through proventriculus to true stomach (ventriculus).
5. Oblique view of valve when closed.
6. Apex of open valve.
7. Ciliated margin of "leaf" of valve.
8. Submentum and glossa, paraglossae, and labial palpi of female; viewed by transmitted light.
9. Maxilla, galea and maxillary palpus of male.
- 10, 11, 12, 13. Dorsal, ventral, lateral and oblique views of genitalia of male.
14. Strigil of female.
15. Calcar of female.

Plate x.

Portion of the railway bank occupied by the huge colony of *Parasphecodes fulviventris* (Fr.). Photograph by the author.